

Emergence of collective dynamical chirality for achiral active particles

Huijun Jiang, Huai Ding, Mingfeng Pu, Zhonghuai Hou*

Department of Chemical Physics & Hefei National Laboratory for Physical Sciences at Microscales, iChEM, University of Science and Technology of China, Hefei, Anhui 230026, China

(Dated: October 4, 2016)

Emergence of collective dynamical chirality (CDC) at mesoscopic scales plays a key role in many formation processes of chiral structures in nature, which may also provide possible routines for people to fabricate complex chiral architectures. So far, most of reported CDCs are found in systems of active objects with individual structure chirality or/and dynamical chirality, and whether CDC can arise from simple and achiral units is still an attractive mystery. Here, we report a spontaneous formation of CDC in a system of both dynamically and structurally achiral particles motivated by active motion of cells. Active moving, confinement and hydrodynamic interaction are found to be the three key factors. Detailed analysis shows that the system can support abundant collective dynamical behaviors, including rotating droplet, rotating bubble, CDC oscillation, array of collective rotation, as well as interesting transitions such as chirality transition, structure transition and state reentrance.

PACS numbers: 05.40.-a, 81.05.Xj

Introduction.—Collective motion of natural or artificial micro(meso)scopic active objects has attracted growing research interests due to its ubiquity and importance in many systems[1–5]. One example is that groups of cells or their fragments can undergo active motion[6–9], and a variety of fundamental processes in development, health and disease depend on such coordinated motions[10–13]. Since active systems can be driven far from equilibrium by continuously consuming energy supplied internally or externally, they are capable of completely altering the collective dynamical behaviors of interacting motile particles in a fashion that is forbidden for non-active particles.

Collective dynamical chirality (CDC)—mirror asymmetry of the collective motion of motile objects—is one of such interesting behaviors supported in active systems. On the one hand, CDC plays a crucial role in many processes in nature. For instance, establishment of left-right asymmetry in embryonic development, one of the most intriguing biological phenomena, involves coordinated activity of many cells[14, 15] where the ability of cells to distinguish between left and right is evident in systems of chiral patterns formed by collective motion of identical cells confined in circular island or ring/stripe-shaped micropatterns[16–19]. On the other hand, CDC may also inspire new routines for fabrication of complex chiral architectures by dynamically self-assembling simple and achiral building blocks[20], e.g., chiral clusters of asymmetric colloidal dimers have been successfully assembled by using alternating current electric fields[21]. Revealing how CDC arises from groups of active units is then very important for the understanding of the formation mechanism.

So far, CDC can be found in systems of active objects with individual structure chirality and/or individual dynamical chirality. For example, CDC has been reported

in several experiments where vortexes were observed for microtubules[22], actin filaments[23], or sperm cells[24] moving on a planar surface. It is believed that individual dynamical chirality might be caused by the rotation of the microtubule around its axis[25] or by the special slender shape[26], while interactions between active objects help to align their moving direction[22, 24, 27]. Besides, man-made catalytical nanorods[28, 29], self-motile colloids[30] or rotating disks[5] can also be dynamically chiral in the form of swimming in circles, and hydrodynamic interaction can synchronize them to form CDC[5]. For structurally chiral objects, dynamical chirality will arise when they are driven by external fields through potential landscapes, and CDC can provide an efficient method for chirality sorting[31–34]. Very recently, a metastable CDC is reported in a system with achiral interaction[35]. Since such a metastable chiral state will relax to a more stable state for a finite temperature, the findings provide very limited help to the understanding of chirality formation in nature as well as new routines for chiral structure fabrication. Consequently, it is still a very attractive mystery that whether stable CDC can emerge in systems of simple particles without both individual structure chirality and dynamical chirality.

Here, we employ a model motivated by active motion of cells in fluid environment, consisting of three elementary ingredients, i.e., achiral active moving, confined space for particle motion and hydrodynamic interaction (HI) between particles, to avoid other complexity such as special shape or structure chirality in real systems which perplexes us to understand the fundamental mechanism underlying formation of CDC[20]. Remarkably, we find that CDC emerges spontaneously in the form of collective rotating for active forces larger than a critical value, near which an interesting oscillation between clockwise and anti-clockwise rotation is observed. Detailed analysis reveals that confinement and HI, along with the active motion of particles, are sufficient for the formation of CDC, while other details such as confinement shape and boundary condition are not relevant. Moreover, phase

*Corresponding Author: hzhjlj@ustc.edu.cn

diagram shows that the system supports abundant collective states, e.g., two distinct states of CDC, a rotating droplet state and a rotating bubble state, are identified by a structure transition of CDC states, and interesting transition behaviors such as state reentrance from fluid-like state to rotating droplet then back to fluid-like state can also be observed. In addition, we find that the number of collective rotation is determined by the width/length ratio of the confinement: A single droplet can be found in squares, while arrays of multiple ones are observed in rectangles.

Model.—We consider a system consisting of N active spherical particles moving in a two-dimensional rectangle confined space of size $L \times W$, where L and W are the length and width, respectively. Active motion of particles is realized by exerting a constant force f_0 along the internal active directions. The only direct interaction between particles is exclusive volume effect taken into account by a repulsive Lennard-Jones potential $U(\mathbf{r}_{ij}) = 4\epsilon \left\{ (2a/r_{ij})^{12} - (2a/r_{ij})^6 \right\} + \epsilon$ existing only if $r_{ij} < 2\sqrt[6]{2}a$, where a is the effective repulsion radius, \mathbf{r}_i the position of particle i , and r_{ij} the distance between i -th and j -th particle. Particles can also interact with each other indirectly by long-range HI through the ambient fluid, where the force on i -th particle generated by the fluid is $\mathbf{F}_{i,fl} = -\gamma[\dot{\mathbf{r}}_i - \mathbf{u}(\mathbf{r}_i, t)]$ with γ the friction coefficient and $\mathbf{u}(\mathbf{r}_i, t)$ the fluid velocity at location \mathbf{r}_i . In our work, $\mathbf{u}(\mathbf{r}_i, t)$ is calculated by a stochastic lattice Boltzmann method where particles are treated as point-like ones[36]. The equations for translational motion of particles with mass m are then

$$m\ddot{\mathbf{r}}_i = f_0\mathbf{n}_i + \mathbf{F}_{i,fl} - \sum_{j=1}^N \frac{\partial U(\mathbf{r}_{ij})}{\partial \mathbf{r}_{ij}} + \xi_i, \quad i = 1, \dots, N. \quad (1)$$

Herein, $\xi_i(t)$ denotes the fluctuation force satisfying the fluctuation-dissipation relation $\langle \xi_i(t)\xi_j(t') \rangle = 2\gamma k_B T \delta(t-t')\delta_{ij}$ where k_B is the Boltzmann constant, T denotes the temperature, and $\mathbf{n}_i = (\cos\theta_i, \sin\theta_i)$ is the direction of active force. Besides, the angle θ_i is steered towards the direction of total force on i -th particle by the rule similar to the one in Ref[37]:

$$\dot{\theta}_i = (1/\tau)[\arg(\ddot{\mathbf{r}}_i) - \theta_i] + \zeta_i \quad (2)$$

where $\arg(\ddot{\mathbf{r}}_i)$ is the angle of total force vector, and $\zeta_i(t)$ is the rotational fluctuation satisfying $\langle \zeta_i(t)\zeta_j(t') \rangle = 3k_B T \delta(t-t')\delta_{ij}/(2a^2\gamma)$. Such a steering rule is motivated by the fact that cells can respond to mechanical forces[9, 38, 39], which is also consistent with reported positive feedback regulation of front-rear cell polarity by actual cell displacements[40, 41]. The persistence time τ for active orientation measures the ability of particles against such external steering, i.e., active direction will yield to the steering very fast for small τ , while tends to keep the internal random behavior for large enough τ similar to the conventional one without steering rule[42, 43].

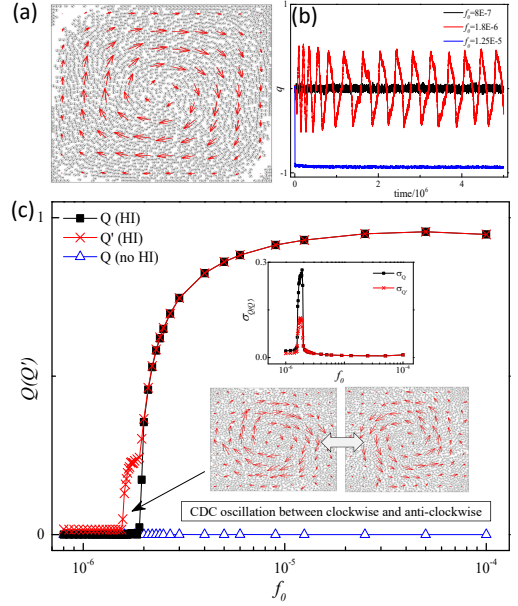


FIG. 1: Spontaneous emergence of collective dynamical chirality. (a) Typical snapshot of CDC state for $f_0 = 1.25 \times 10^{-5}$. Red arrows are locally averaged velocities of particles in the nearest 10×10 grids (normalized by the maximal one). (b) Time series of q for $f_0 = 8 \times 10^{-7}$, 1.8×10^{-6} and 1.25×10^{-5} . (c) Dependence of order parameters Q and Q' on the active force f_0 . Standard deviation of Q is plotted in the top inset and typical snapshots of clockwise and anti-clockwise rotation during chirality oscillation in the bottom. For comparison, Q without hydrodynamic interaction and its standard deviation are also plotted.

We rescale the density, time and length by the particle density, the simulation time step of the lattice Boltzmann method, and the grid length of the lattice, respectively. We fix $k_B T = 10^{-7}$, $\epsilon = 5 \times 10^{-4}$, $a = 0.75$, and $\gamma = (32/3)av\rho$ with fluid viscosity $\nu = 0.1$ and density $\rho = 1$, for which the system will reach a fluid-like state in the absence of active force. The persistence time, active force, number of particles and size of the space are $\tau = 1$, $f_0 = 1.25 \times 10^{-5}$, $N = 2500$ and $L = W = 100$ (corresponding to a volume fraction about 0.442), if not otherwise stated. The interaction between active particles and confined boundary is realized by bounce-back rule.

Result.—To begin, we investigate how the collective motion of particles depends on the magnitude f_0 of the active force. For a small active force, e.g., $f_0 = 8 \times 10^{-7}$, the system is still fluid-like where particles move randomly. Quite interestingly, a CDC state emerges spontaneously if the active force becomes large enough. A typical snapshot of such a state for $f_0 = 1.25 \times 10^{-5}$ is presented in Fig.1(a) where all the particles rotate collectively around the center of the space $\mathbf{r}_c = (L/2, W/2)$. To quantitatively characterize CDC of the system, we define an order parameter

$$q = \frac{1}{N} \sum_{i=1}^N \varphi_i. \quad (3)$$

Here, $\varphi_i = \omega_i/|\omega_i|$ denotes the “dynamical-chirality spin” of particle i , where $\omega_i = (\mathbf{r}_i - \mathbf{r}_c) \times \dot{\mathbf{r}}_i/|\mathbf{r}_i - \mathbf{r}_c|^2$ is the angular velocity of i -th particle relative to \mathbf{r}_c . Note that φ_i equals to 1 for anti-clockwise rotation and -1 for clockwise one. Time-dependencies of q for $f_0 = 8 \times 10^{-7}$ and 1.25×10^{-5} are plotted in Fig.1(b). It can be observed that q fluctuates around a fixed value after a quick relaxation, indicating that the system can finally reach a stable steady state. Time-averaged q equals 0 for the fluid-like state, and is of a negative (or positive) value for the CDC state with collective clockwise (or anti-clockwise) rotation.

To obtain a global picture for how CDC emerges as f_0 increases, magnitude of time-averaged q ,

$$Q = \left| \lim_{t_0 \rightarrow \infty} \frac{1}{t_0} \int_0^{t_0} q(t) dt \right| \quad (4)$$

as a function of f_0 is drawn in Fig.1(c). Clearly, a continuous-like transition from fluid-like state to CDC state induced by particle activity is observed: Q is nearly zero for small forces and quickly increases to be nearly 1 for f_0 larger than a threshold $f_c \simeq 1.9 \times 10^{-6}$ where the standard deviation σ_Q exhibits a clear-cut peak as shown in the top inset of Fig.1(c). The presence of f_c may be understood by the following observations. Collective rotation can lead to accumulation of particles near the boundary (Fig.1(a)), which in return provides a tendency for particles to diffuse collectively on the opposite direction and consequently an effective barrier for emergence of CDC.

Remarkably, we also observe an interesting oscillation of CDC. As depicted in Fig.1(b), particles rotate periodically between clockwise and anti-clockwise for an active force slightly smaller than f_c , e.g., $f_0 = 1.8 \times 10^{-6}$, whose typical snapshots are shown in the bottom-left and bottom-right insets of Fig.1(c) and a supplemental video is provided at [URL will be inserted by publisher] for a multimedia view. Based on the same physical picture as discussed above, a possible mechanism for the CDC-oscillation can be concluded as follows. For such a force near f_c , a weak collective rotation of active particles can be induced by noise, which however cannot overcome the barrier formed by accumulation of particles near the boundary. Notice that, collective diffusion of particles on the opposite direction is still available, and consequently an collective rotation with opposite chirality is formed, for which same things repeated.

To identify the region of CDC oscillation, the time-averaged magnitude of q , $Q' = \lim_{t_0 \rightarrow \infty} (1/t_0) \int_0^{t_0} |q(t)| dt$, is presented in Fig.1(c). It can be found that Q' is overlapped with Q very well for small or large active forces. In the CDC region where active force is in the range $1.55 \times 10^{-6} < f_0 < f_c$, $Q = 0$ indicates that there is no time-averaged CDC, while

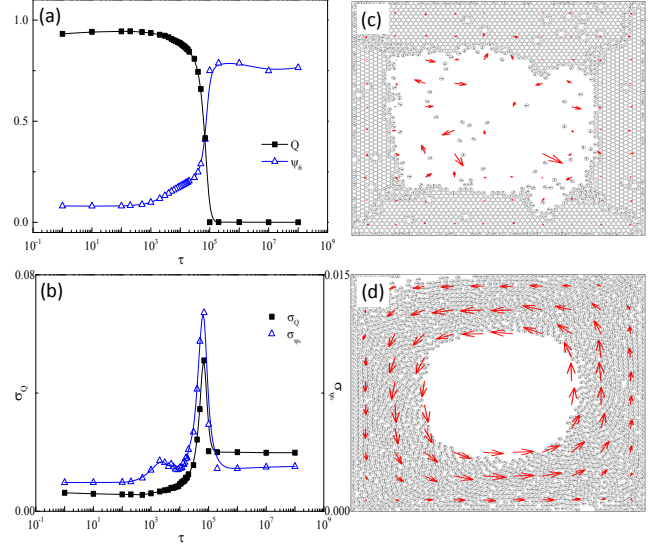


FIG. 2: (a) Dependence of order parameters Q and Ψ_6 on persistence time τ . (b) Standard deviation of order parameters as functions of τ . (c) Typical snapshots of crystal-like state for $\tau = 10^8$ and (d) rotating bubble state for $\tau = 10^4$. The locally averaged velocities of particles normalized by the maximal one are presented by red arrows.

Q' is larger than zero obviously, demonstrating that particles do rotate collectively for a given time. The standard deviation of Q' is also plotted in the top inset of Fig.1(c), which shows a peak at $f_0 \simeq 1.9 \times 10^{-6}$ as same as the one of Q , demonstrating again that chirality oscillation is not a new dynamical phase of the system but an oscillation of noise-induced CDC.

One may be wondering what are the key ingredients that lead to the above interesting observations. In fact, we find that besides the active driving, the long range HI and space confinement are two other necessary conditions for emergence of CDC as well as the CDC-oscillation. To show this, we have performed parallel simulations with the same parameter settings as above but with the HI turned off by using Brownian dynamics where diffusion coefficient of a free-diffusion particle is ensured to be the same. The obtained Q without HI is plotted in Fig.1(c) to be compared with the one with HI. Clearly, there is no CDC can be observed for all range of parameters. We also repeat similar simulations for collective motion of particles without confinement, and no CDC is found, too. What's more, other rules of interaction between active particles and confined boundary such as reflecting rule are also tested, and our findings are not sensitive to the boundary condition. In short, HI and confinement, along with activity of particles are the three key factors for the emergence of CDC.

It is noted that, dynamics of active particles may change dramatically for different persistence time for active direction, thus, we now try to figure out how τ affects collective motion of active particles. In Fig.2(a), Q as a function of τ is plotted by fixing $f_0 = 1.25 \times 10^{-5}$, where

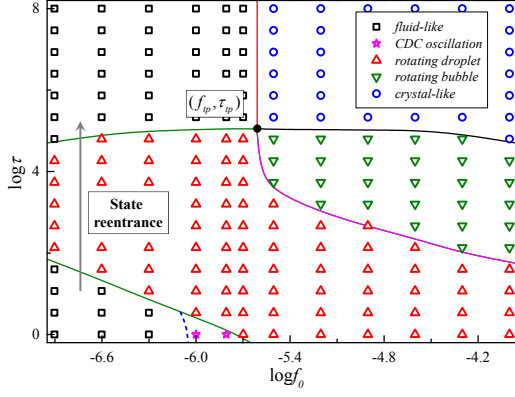


FIG. 3: Phase diagram on $f_0 - \tau$ plane. There is a triple-point-like point (f_{tp}, τ_{tp}) above which no CDC can be formed for $\tau > \tau_{tp}$, and a state reentrance from fluid-like state to rotating droplet state then back to fluid-like state can be found as indicated by the gray arrow.

a transition between CDC and an achiral state can also be found. A typical snapshot of the achiral state is presented in Fig.2(c). Different to the fluid-like state, the achiral state observed here is crystal-like where particles are arranged in hexagonal ordering. The ordering can be measured by[44]

$$\Psi_6 = \frac{1}{N} \sum_{m=1}^N \frac{1}{N_m} \sum_{l=1}^{N_m} \exp(6i\theta_{ml}), \quad (5)$$

where i is the imaginary unit, θ_{ml} is the angle between an arbitrary reference axis and the displacement vector between particles m and l , and the sum runs over the nearest $N_m = 6$ particles within a cutoff radius of $2.6a$ from particle m (for particles adjacent to the confined boundary, only $N_m = 4$ neighbors are needed). to form hexagonal ordering. In Fig.2(a), Ψ_6 increases from a value near 0 to about 1 as τ increases, indicating a structure transition when collective motion of particles changes CDC state to crystal-like state.

If one takes a closer look at the dependence of Ψ_6 on τ , it can be found that there seems to be a shoulder before the transition happens. For more detailed information, standard deviations σ of Q and Ψ_6 are given in Fig.2(b). As expected, peaks are observed for both σ_Q and σ_{Ψ_6} at $\tau_c \simeq 7 \times 10^4$, corresponding to the transition of both chirality and structure from CDC state to crystal-like state. It is quite interesting that there is also another peak of σ_{Ψ_6} at $\tau_s \simeq 2 \times 10^3$ where no peaks of σ_Q are found, i.e., the CDC state undergoes a structure transition without loss of chirality. By comparison between the snapshot for $\tau = 1 < \tau_s$ in Fig.1(b) and a typical snapshot presented in Fig.2(d) for $\tau_s < \tau = 10^4 < \tau_c$, we can mark the two states of CDC as rotating droplet for the former and rotating bubble for the later.

In order to explore fully how parameters affect particles' collective motion, a phase diagram in $f_0 - \tau$ plane

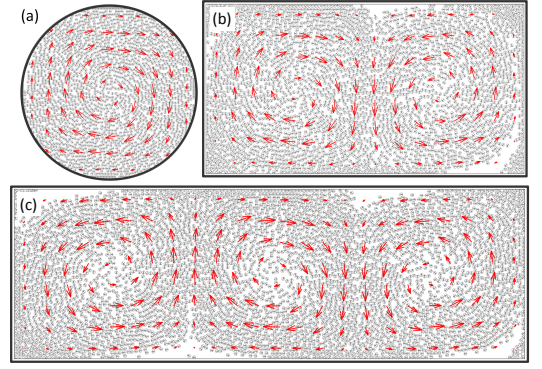


FIG. 4: Collective dynamical chirality for different boundary shapes. (a) Circle with diameter 100, and rectangles with (b) 160×80 and (c) 240×80 for $f_0 = 1.25 \times 10^{-5}$ and $\tau = 1$.

is obtained by extensive simulations (Fig.3), and several interesting remarks can be made. Firstly, there is a triple-point-like point located at (f_{tp}, τ_{tp}) where CDC state meets both fluid-like and crystal-like state. For $\tau < \tau_{tp}$, CDC can arise spontaneously, while for larger τ s only fluid-like state and crystal-like state can be observed. Notice that the steering rule in Eq.(2) can be neglected for large enough τ , the observation is in good agreement with findings reported in literature[42, 43]. Secondly, structure transition between the two states of CDC, rotating droplet and rotating bubble, occurs only for $f_0 > f_{tp}$, below which rotating droplet is the sole CDC state. Lastly, the system can also support other interesting state transition behaviors. As indicated by the gray arrow in Fig.2(e), a state reentrance can be found as τ increases for $f_0 < f_{tp}$, i.e., particles are firstly fluid-like for small τ s then change to be of CDC for intermediate τ s, then back to be fluid-like when τ is large enough.

At last, effects of confinement shape on CDC are also considered. A typical snapshot for collective motion of particles in a circular confined space with diameter 100 is shown in Fig.4(a). Similarly, CDC emerges for the same parameters as in the square one, indicating that formation of CDC is not sensitive to the confinement shape. Dynamics of particles in confinement with different length/width ratio is also investigated. Typical snapshots for $L \times W = 160 \times 80$ and 240×80 are presented in Fig.4(b) and Fig.4(c), respectively, where number of particles is set to be $N = 3200$ for the former and $N = 4800$ for the later to keep the volume fraction unchanged. Interestingly, array of vortices with opposite chirality for adjacent ones is observed, and the number of vortices seems to be proportional to the length/width ratio.

Conclusion.-In summary, it was revealed that active motion, space confinement and hydrodynamic interaction are sufficient for the emergence of CDC in a system of active particles without individual structure chirality and dynamical chirality. CDC states were found to be formed via a chirality transition from other achiral state such as fluid-like state or crystal-like state, while they can also undergo a structure transition to form two dis-

tinct states, i.e., a rotating droplet and a rotating bubble. Phase diagram showed that CDC formation is controlled by the active force and the persistence time for particles to maintain their internal motion. Since emergence of CDC underlies many formation processes of chiral structures, our finding may inspire experimental studies to explore new routines for fabrication of complex chiral architectures by simple and achiral units, and shed light on the understanding of chirality formation in other complex

systems such as establishment of left-right asymmetry in embryonic development.

Acknowledgments.—This work is supported by National Basic Research Program of China (Grant No. 2013CB834606), by National Science Foundation of China (Grant Nos. 21125313, 21521001, 21473165, 21403204), and by the Fundamental Research Funds for the Central Universities (Grant Nos. WK2060030018, 2030020028, 2340000074).

-
- [1] M. Marchetti, J. F. Joanny, S. Ramaswamy, T. B. Liverpool, J. Prost, M. Rao, and R. A. Simha, *Reviews of Modern Physics* **85**, 1143 (2013).
 - [2] J. Elgeti, R. G. Winkler, and G. Gompper, *Reports on progress in physics* **78**, 056601 (2015).
 - [3] H. Wioland, F. G. Woodhouse, J. Dunkel, and R. E. Goldstein, *Nature Physics* **12**, 341 (2016).
 - [4] E. Lushi, H. Wioland, and R. E. Goldstein, *Proc. Natl. Acad. Sci. USA* **111**, 9733 (2014).
 - [5] Y. Goto and H. Tanaka, *Nature communications* **6**, 5994 (2015).
 - [6] R. Ananthakrishnan and A. Ehrlicher, *Int J Biol Sci* **3**, 303 (2007).
 - [7] G. F. Weber, M. A. Bjerke, and D. W. DeSimone, *Developmental cell* **22**, 104 (2012).
 - [8] K. Sato, T. Hiraiwa, and T. Shibata, *Physical review letters* **115**, 188102 (2015).
 - [9] D. T. Tambe, C. C. Hardin, T. E. Angelini, K. Rajendran, C. Y. Park, X. Serr-Picamal, E. H. Zhou, M. H. Zaman, J. P. Butler, D. A. Weitz, et al., *Nature Materials* **10**, 469 (2011).
 - [10] K. R. Levental, H. Yu, L. Kass, J. N. Lakins, M. Egeblad, J. T. Erler, S. F. Fong, K. Csiszar, A. Giaccia, W. Weninger, et al., *Cell* **139**, 891 (2009).
 - [11] A. Bianco, M. Poukkula, A. Cliffe, J. Mathieu, C. M. Luque, T. A. Fulga, and P. Rørth, *Nature* **448**, 362 (2007).
 - [12] P. Friedl and D. Gilmour, *Nature reviews Molecular cell biology* **10**, 445 (2009).
 - [13] D. J. Montell, *Science* **322**, 1502 (2008).
 - [14] M. Blum, K. Feistel, T. Thumberger, and A. Schweickert, *Development* **141**, 1603 (2014).
 - [15] J.-B. Coutelis, N. González-Morales, C. Géminard, and S. Noselli, *EMBO reports* p. e201438972 (2014).
 - [16] L. Q. Wan, K. Ronaldson, M. Park, G. Taylor, Y. Zhang, J. M. Gimble, and G. Vunjak-Novakovic, *Proceedings of the National Academy of Sciences* **108**, 12295 (2011).
 - [17] H. Yamanaka and S. Kondo, *Genes to Cells* **20**, 29 (2015).
 - [18] A. Tamada, S. Kawase, F. Murakami, and H. Kamiguchi, *The Journal of cell biology* **188**, 429 (2010).
 - [19] J. Xu, A. Van Keymeulen, N. M. Wakida, P. Carlton, M. W. Berns, and H. R. Bourne, *Proceedings of the National Academy of Sciences* **104**, 9296 (2007).
 - [20] A. Guerrero-Martínez, J. L. Alonso-Gómez, B. Auguié, M. M. Cid, and L. M. Liz-Marzán, *Nano Today* **6**, 381 (2011).
 - [21] F. Ma, S. Wang, D. T. Wu, and N. Wu, *Proceedings of the National Academy of Sciences* **112**, 6307 (2015).
 - [22] Y. Sumino, K. H. Nagai, Y. Shitaka, D. Tanaka, K. Yoshikawa, H. Chaté, and K. Oiwa, *Nature* **483**, 448 (2012).
 - [23] V. Schaller, C. Weber, C. Semmrich, E. Frey, and A. R. Bausch, *Nature* **467**, 73 (2010).
 - [24] I. H. Riedel, K. Kruse, and J. Howard, *Science* **309**, 300 (2005).
 - [25] O. Kagami and R. Kamiya, *Journal of Cell Science* **103**, 653 (1992).
 - [26] H. Jiang and Z. Hou, *Soft Matter* **10**, 1012 (2014).
 - [27] H. Jiang and Z. Hou, *Soft matter* **10**, 9248 (2014).
 - [28] P. Dhar, T. M. Fischer, Y. Wang, T. Mallouk, W. Paxton, and A. Sen, *Nano letters* **6**, 66 (2006).
 - [29] L. Qin, M. J. Banholzer, X. Xu, L. Huang, and C. A. Mirkin, *Journal of the American Chemical Society* **129**, 14870 (2007).
 - [30] J. Gibbs, S. Kothari, D. Saintillan, and Y.-P. Zhao, *Nano letters* **11**, 2543 (2011).
 - [31] M. Kostur, M. Schindler, P. Talkner, and P. Hänggi, *Physical review letters* **96**, 014502 (2006).
 - [32] D. Speer, R. Eichhorn, and P. Reimann, *Physical review letters* **105**, 090602 (2010).
 - [33] L. Bogunovic, M. Flidner, R. Eichhorn, S. Wegener, J. Regtmeier, D. Anselmetti, and P. Reimann, *Physical review letters* **109**, 100603 (2012).
 - [34] A. Nourhani, V. H. Crespi, and P. E. Lammert, *Physical Review Letters* **115**, 118101 (2015).
 - [35] R. E. Breier, R. L. B. Selinger, G. Ciccotti, S. Herminghaus, and M. G. Mazza, *Physical Review E* **93**, 022410 (2016).
 - [36] P. Ahlrichs and B. Dünweg, *International Journal of Modern Physics C* **9**, 1429 (1998).
 - [37] E. Mones, A. Cziráok, and T. Vicsek, *New journal of physics* **17**, 063013 (2015).
 - [38] M. M. Kozlov and A. Mogilner, *Biophysical journal* **93**, 3811 (2007).
 - [39] P. T. Yam, C. A. Wilson, L. Ji, B. Hebert, E. L. Barnhart, N. A. Dye, P. W. Wiseman, G. Danuser, and J. A. Theriot, *The Journal of cell biology* **178**, 1207 (2007).
 - [40] A. T. Dawes and L. Edelstein-Keshet, *Biophysical journal* **92**, 744 (2007).
 - [41] A. Szabó, R. Ünneper, E. Méhes, W. Twaal, W. Argraves, Y. Cao, and A. Cziráok, *Physical biology* **7**, 046007 (2010).
 - [42] T. Speck, J. Bialké, A. M. Menzel, and H. Löwen, *Physical Review Letters* **112**, 218304 (2014).
 - [43] R. Ni, M. A. C. Stuart, and P. G. Bolhuis, *Physical review letters* **114**, 018302 (2015).
 - [44] J. Stenhammar, R. Wittkowski, D. Marenduzzo, and M. E. Cates, *Physical review letters* **114**, 018301 (2015).